Environ Biol Fish (2015) 98:477–486
DOI 10.1007/s10641-014-0278-z

Habitat simplification increases the impact of a freshwater invasive fish

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Received: 9 December 2013 / Accepted: 29 April 2014 / Published online: 11 May 2014

Abstract Biodiversity continues to decline at a range of spatial scales and there is an urgent requirement to understand how multiple drivers interact in causing such declines. Further, we require methodologies that can facilitate predictions of the effects of such drivers in the future. Habitat degradation and biological invasions are two of the most important threats to biodiversity and here we investigate their combined effects, both in terms of understanding and predicting impacts on native species. The predatory largemouth bass *Micropterus salmoides* is one of the World's Worst Invaders, causing declines in native prey species, and its introduction often coincides with habitat simplification. We investigated the predatory functional response, as a measure of ecological impact, of juvenile largemouth bass in artificial vegetation over a range of habitat complexities (high, intermediate, low and zero). Prey, the female guppy *Poecilia reticulata,* were representative of native fish. As habitats became less complex, significantly more prey were consumed, since, even although attack rates declined, reduced handling times resulted in higher maximum feeding rates by bass. At all levels of habitat complexity, bass exhibited potentially population destabilising Type II functional responses, with no emergence of more stabilising Type III functional responses as often occurs in predator-prey relationships in complex habitats. Thus, habitat degradation and simplification potentially exacerbate the impact of this invasive species, but even highly complex habitats may ultimately not protect native species. The utilisation of functional responses under varying environmental contexts provides a method for the understanding and prediction of invasive species impacts.

Keywords Habitat complexity · Invasive species · Functional response · Impact · Global change · Freshwater fish

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Introduction

Biodiversity at global, regional and local scales is declining and the conservation of natural resources is under threat from a number of drivers of global change

(Sala et al. 2000; Thomas et al. 2004; Mokany et al. 2012). Such processes are of particular concern in freshwater systems, with drivers such as habitat alteration and invasions by non-native species identified as significant stressors (Saunders et al. 2002; Dudgeon et al. 2006). The modification of freshwater habitats results from a range of human-mediated processes including changes to flow regimens (Bunn and Arthington 2002), dam construction (Nilsson and Berggen 2000), and destruction of vegetation (Radomski and Goeman 2001). Similarly, biological invasions are increasing due to a wide range of human-mediated vectors and pathways (Levine and D'Antonio 2003). In freshwaters, invasive species modify ecosystems through a range of processes including competitive exclusion (Rowles and O'Dowd 2006) and predation (Griffen and Delaney 2007), which may result in dramatic changes to native communities (Crooks 1998).

One of the main challenges in ecology is the ability to predict how drivers of global change, such as biological invasions, may impact ecosystems (Parker et al. 1999; Ricciardi et al. 2013; Dick et al. 2014). Furthermore, research often considers and examines these drivers as independent, single entities (Fazey et al. 2005), however, there is an emerging realisation that biodiversity loss will be better understood and predicted when the relative roles of the major drivers are considered in combination (Facon et al. 2006). It is also recognised that drivers may act synergistically through a variety of pathways (Didham et al. 2007). For example, changes in the traits of an invasive species with habitat alterations, such as predatory efficiency, might result in changes in *per capita* effects with potential wide-ranging consequences for native species population dynamics (Parker et al. 1999).

In aquatic systems, the role of habitat structure, such as that provided by algae and macrophytic plants, is well documented in inter- and intraspecific interactions from a wide range of taxa (Boström et al. 1999; Saha et al. 2009; Gosnell et al. 2012). For a number of fish species in particular, habitat structure has been shown to mediate impacts of fish predation by, for example, creating a physical barrier to predator movement (Savino and Stein 1982). Mediatory effects may also occur in such interactions due to the provision of refuge space for prey (Persson and Eklöv 1995; Beukers and Jones 1997; Anderson 2001; Almany 2004a). Therefore, the loss of structural complexity resulting from habitat degradation may reduce prey survival due to increased predation vulnerability (Nelson and Bonsdorff 1990). However, predators that adopt a sit-and-wait strategy of prey capture may perform less efficiently with degradation of habitat, reducing predation success (Flynn and Ritz 1999).

A promising methodology that not only provides an understanding of predator-prey interactions but allows predictions of invasive species impact is to examine the functional response (Dick et al. 2013, 2014; Alexander et al. 2014), that is, the relationship between prey density and predator consumption rate (Solomon 1949; Holling 1959). Such a focus allows important density-dependent effects of predation on population stability to be examined owing to the different contributions of response Types (I, II or III) to population dynamics (Murdoch and Oaten 1975). In a Type I response, predator consumption increases linearly with prey number until a threshold density plateau is reached. However, under certain ranges of prey density, a Type II inversely density-dependent response can result in an increase in mortality risk to prey with decreasing density (Hassell 1978). This is in contrast to reduction in mortality risk when prey density declines in a Type III response (Hassell 1978). This is particularly important in habitat complexity studies, where changes in structure can result in alterations to the functional response Type and hence prey population viability (Lipcius and Hines 1986; Buckel and Stoner 2000; Alexander et al. 2012). Furthermore, the application of functional responses in invasion biology has been demonstrated to be effective, with higher functional responses of invasive species compared to natives in laboratory studies corroborated by results from field studies (Bollache et al. 2008; Dick et al. 2013). Here, we use functional responses to predict the impact that changes in habitat complexity, representative of those resulting from habitat destruction, may have on the predator-prey dynamics of an invasive fish predator, one of the "World's Worst Invaders" (ISSG 2013), on prey species.

As a result of its popularity as an angling species, the largemouth bass *Micropterus salmoides* is one of the five globally most introduced fish species (Welcomme 1992) and, where such introductions have occurred, predation by this species has a major impact on fish communities (Godinho and Ferreira 2000; Ellender et al. 2011; Almeida et al. 2012). In South Africa and in the Iberian Peninsula in southern Europe, for example, largemouth bass are a well-established invasive species that have subsequently invaded a number of

headwater streams, where many native fish species are now endangered or absent (Ellender et al. 2011; Almeida et al. 2012). In addition to this, such systems are also facing a double threat of habitat degradation due to destruction of natural vegetation (Saunders et al. 2002). As ambush predators, largemouth bass typically use structural littoral habitats including aquatic vegetation (Savino and Stein 1989a), and juveniles in particular predominantly select such environments (Olson et al. 2003). We therefore manipulated simulated-habitat complexity along a prey density gradient in order to ask questions regarding the density-dependence of impact of this invasive predator on prey population in the context of habitat degradation.

The aim of this study was thus to describe and quantify the functional responses, and hence impacts, of juvenile largemouth bass on a prey species, the guppy *Poecilia reticulata*, that served as a commercially available surrogate for endangered fish found in headwater systems, with respect to varying levels of habitat complexity. The aims were to establish whether: (1) juvenile largemouth bass exhibit predatory functional responses towards small fish prey; (2) the functional response Type is habitat dependent; and (3) varying habitat complexity alters the strength of the functional response.

Materials and methods

Collection and maintenance of experimental animals

Juvenile largemouth bass *Micropterus salmoides* were collected in June 2013 by electrofishing from Douglas Dam (33°19'16"S; 26°31'15" E) and Grey Dam (33°19'29."S; 26°31'39" E), Grahamstown, South Africa. All fish were transported to the Department of Ichthyology and Fisheries Science (DIFS), Rhodes University, Grahamstown and were housed in 600 L tanks in a closed recirculating system. Fish were allowed to acclimate for at least one week prior to use in predation trials and were maintained on a diet of earthworms. As earthworms were not the focal prey species used in the experiment, this diet ensured that no prior prey learning occurred in holding tanks. Prey used were females of the guppy *Poecilia reticulata* (15–20 mm total length), sourced from a captive breeding stock at the DIFS. Female guppies were selected over males owing to their inconspicuous colouration. Guppies were housed in two 600 L tanks and were fed daily on commercially available fish food.

Experimental set up

Functional response experiments were conducted in 15 square (1,000 mm) 300 L fibreglass tanks that were part of the same flow-through system as the holding tanks described above (water flow 1 L min^{-1}; 23.01±0.17ºC, mean temperature ± SE). Tank depth was 370 mm with water level at 300 mm at the central outflow pipe (see Jones 2003 for further detail). In the centre of each tank there was an outlet for water overflow that was covered with mesh and secured with cable ties to prevent predators and/or prey escaping. To reduce potential stress on the fish, each tank was half covered with a dark screen to provide a darkened refuge. An airline provided further aeration of water in the tank in addition to the aerated inflowing water from the recirculating system during predation trials.

To simulate habitat structure, strips of green polyethylene (40 mm long and 15 mm wide) were tied in a uniform arrangement to green plastic mesh, cut to fit the bottom of the aquarium. The mesh was then weighted to the bottom of the tanks. This allowed the artificial vegetation to float upwards and occupy the entire water column in the same way as rooted aquatic plants in freshwater systems (personal observation). A plant mimic was used here to allow for standardisation of cover. Densities of vegetation represented high (2,700 blades m^{-2}), medium (1,800 blades m^{-2}), low (900 blades m^{-2}) and zero habitat complexities. To control for the presence of mesh contributing a further element of habitat complexity, mesh without artificial plants was added in zero complexity treatments.

Bass (n=18) were selected from a relatively uniform size class to reduce the influence of size-related differences in prey consumption (86.86±2.49 mm, mean total length ± SE; 14.0±0.38 mm, mean gape height ± SE). Gape height was measured by opening the mouth to its maximum capability without distortion or stretching of the jaws and taking a measurement using callipers. Bass were reused in the four habitat treatments (detailed below), however, we ensured that each individual predator was used a maximum of four times and only once within each prey density in each habitat complexity. At least two days recovery time was allowed between uses.

Functional response trials

Bass were randomly selected from their holding tanks 24 h prior to a trial and transferred to an experimental tank, where they were held without food to allow for acclimatisation and standardisation of hunger levels. Individual fish were then presented with guppies at six prey densities (2, 4, 8, 16, 32, 64), with at least three replicates per density. Feeding trials were initiated at 10:00 h and prey consumption was examined after four hours. Controls were three replicates of each prey density in the absence of predators at each of the habitat complexities.

Statistical analysis

All analysis was carried out in R v. 2.15.1 (R Development Core Team 2012). Differences in overall prey consumption among habitat complexities and prey densities were assessed using a generalised linear model (GLM) with binomial error distribution. As no interaction was found between habitat complexity and prey density, the interaction term was removed to identify the minimum adequate model (Crawley 2007). Significant effects in the model were analysed with Tukey's contrast *post hoc* tests, performed using the package Multcomp 1.2–8 (Hothorn et al. 2008).

In the assessment of a predator's functional response, there is a range of models and choice is based on whether a particular study takes a mechanistic or phenomenological approach (Jeschke et al. 2002). Although mechanistic application of parameters such as attack rate and handling time should be supported with empirical measurements of such estimates (Caldow and Furness 2001; Jeschke and Hohberg 2008), the phenomenological use of these parameters provides a tool to examine differences in functional response Types and magnitudes in comparative experiments, as is the approach taken here (Alexander et al. 2013; Dick et al. 2013, 2014; MacNeil et al. 2013).

We first determined the functional response Type using logistic regression, testing for a negative linear coefficient (fitted using maximum likelihood) in the relationship between the proportion of prey eaten and prey density that indicates a Type II response (Trexler et al. 1988; Juliano 2001). Further, we estimated values of '*a*' (attack rate), '*h*' (handling time) and maximum feeding rate ($1/hT$, where T=experimental period) using the 'random predator equation' (Rogers 1972), which is appropriate where prey are not replaced as they are consumed (Juliano 2001);

$$N_e = N_0\{1-\exp[a(N_e h - T)]\}$$

where N_e is the number of prey eaten, N_0 is the initial density of prey, a is the attack constant, h is the handling time and T is the experimental period. Due to the implicit nature of the random predator equation, the Lambert W function was implemented to fit the model to the data (Bolker 2008). Bootstrapping was used to generate multiple estimates (n=30) of the response parameters of attack rate a, handling time h and maximum feeding rate ($1/hT$), which were then compared between habitat complexities in a GLM with Tukey's contrast *post hoc* tests.

Results

In control groups with no predators, prey survival was always >98 % in each of the habitat treatments. Experimental deaths were therefore attributed to predation by juvenile largemouth bass. As habitat became less complex, significantly more prey were eaten ($F_{3,\ 68}$=8.41, p<0.001; Fig. 1), and bass in the highest habitat complexity consumed significantly less prey compared to all other habitat complexities (Tukey's contrasts, p<0.01; Fig. 1). There were no differences in prey consumed between intermediate, low and zero habitat complexities. Significantly more prey were consumed at higher as compared to lower densities ($F_{5,\ 68}$=76.88, p<0.001).

Logistic regression indicated that, in each of the habitat complexities, largemouth bass exhibited a Type II functional response towards prey, as revealed by significantly negative linear coefficients (Table 1; Fig. 2a-d). As habitat became less complex, attack rate a significantly declined ($F_{3,\ 116}$=26.28, p<0.001; Fig. 3a). In comparison to low and intermediate habitats, which did not differ from each other, attack rate was significantly reduced in zero habitat treatments, and significantly greater in high complexity treatments (Tukey's contrasts, all p<0.01; Fig. 3a). Again as habitat became less complex, handling time h declined ($F_{3,\ 116}$= 151.12, p<0.001), and was greatest in high complexity in comparison to the other treatments (Tukey's contrasts, all p<0.01; Fig. 3b). This was also reflected in an increase in maximum feeding rate ($F_{3,\ 116}$=99.09, p<0.001), that was greatest for zero and low habitat

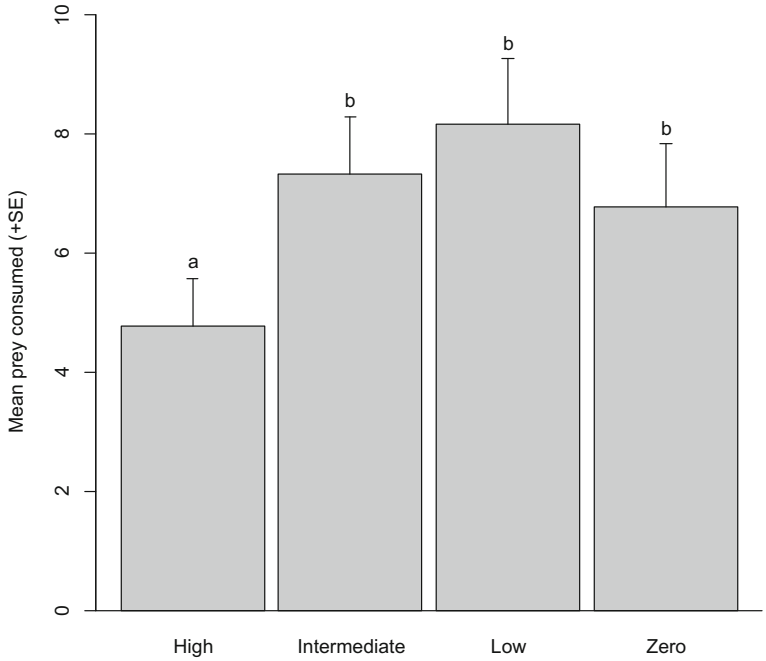

Fig. 1 Mean prey consumed (+SE) by juvenile largemouth bass in high, intermediate, low and zero complexity simulated habitats. Different letters above bars indicate significant differences (Tukey's contrasts, $p<0.01$)

complexities, and lowest in high complexity treatments (Tukey's contrasts, all $p<0.01$; Fig. 3c).

Discussion

Freshwater systems are threatened by a number of drivers of global change (Sala et al. 2000; Buisson et al. 2013) and, around the world, formerly pristine headwater stream environments are impacted by both habitat destruction and invasions by non-native species (Impson et al. 2002; Ellender et al. 2011). Such drivers have important consequences when considered individually, however, they may also act in combination to result in greater, synergistic impacts to native populations (Didham et al. 2007). Furthermore, there is a pressing requirement to predict such impacts of both established and emerging invasive species under a range of environmental conditions such that appropriate mitigation and control measures may be implemented (Byers et al. 2002; Simberloff et al. 2013; Alexander et al. 2014; Dick et al. 2014).

Reduction in habitat complexity significantly increased consumption rates by invasive juvenile largemouth bass *Micropterus salmoides* of the female guppy *Poecilia reticulata*. We have thus demonstrated that the impact by juvenile largemouth bass, one of the "100 World's Worst" invaders (ISSG 2013), may be heightened with degradation of habitat. In addition, we found that between zero to intermediate structural

Table 1 Parameter estimates (and significance levels) from logistic regression analyses of proportion of prey consumed against initial prey density, in high, intermediate, low and zero habitat complexities. Values for the intercept and linear (N_0) terms are presented with p values

Habitat complexity	Intercept (p value)	N_0 (p value)	Functional response type
High	0.21 ($p=0.39$)	−0.04 ($p<0.001$)	II
Intermediate	2.04 ($p<0.001$)	−0.07 ($p<0.001$)	II
Low	1.73 ($p<0.001$)	−0.05 ($p<0.001$)	II
Zero	0.73 ($p<0.01$)	−0.04 ($p<0.001$)	II

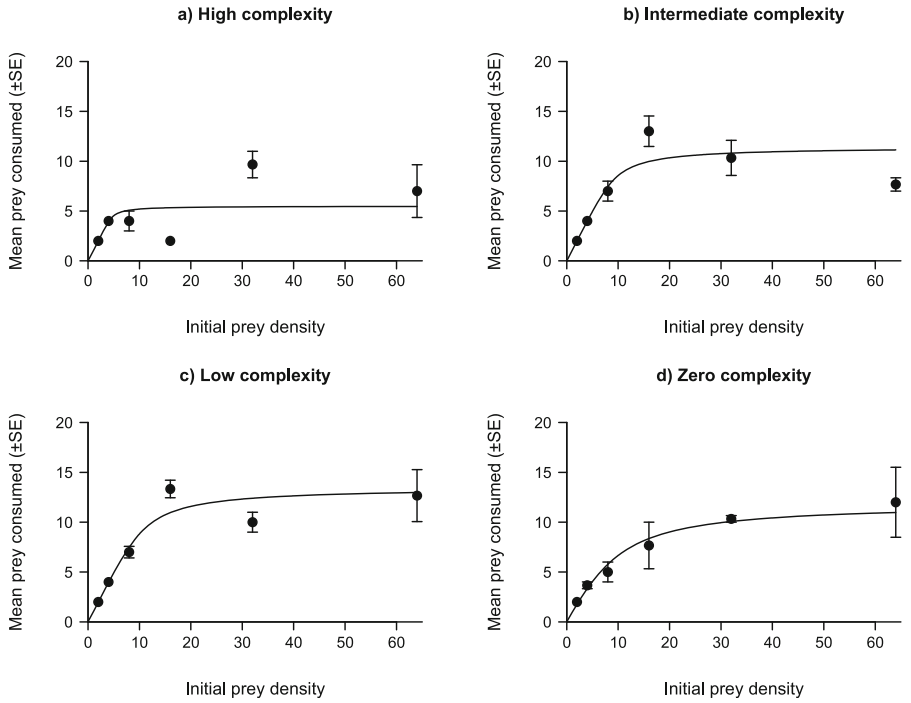

Fig. 2 Functional responses of juvenile bass towards prey in **a** high, **b** intermediate, **c** low and **d** zero habitat complexity (as modelled by the Rogers random predator equation for a Type II response). Data are mean number of prey consumed at each density ± SE

complexities, there was no significant difference in the numbers of prey consumed. This suggests the occurrence of a threshold in complexity between the intermediate and high-complexity experimental habitats that can reduce the efficiency of the predator (Coull and Wells 1983; Gotceitas and Colgan 1989; Manatunge et al. 2000). This may in turn have important consequences for predatory behaviours in instances where predators alter their foraging modes in response to changes in their surrounding environment (Scharf et al. 2006). There may also be additional consequences for predator-prey dynamics due to effects on predator-predator interactions, potentially influencing facilitation or interference outcomes (Sih et al. 1998; Warfe and Barmuta 2004).

In each of the four levels of habitat complexity, juvenile bass exhibited a Type II functional response towards the fish prey. This is counter to a number of studies demonstrating how variations in environment, such as habitat complexity, light intensity and temperature (Eggleston 1990; Koski and Johnson 2002; Alexander et al. 2012), may result in changes towards Type III responses. Generally changes in functional response types occur when factors, such as environmental conditions, affect the searching ability of a predator. These are generally most influential at low prey densities (Crowder and Cooper 1982; Heck and Crowder 1991) and habitat complexity is often an important determinant of such outcomes (Buckel and Stoner 2000; Kushner and Hovel 2006; Alexander et al. 2012). Such a change in functional response can be significant when considering population stability and viability, as Type II responses can drive prey populations to local extinction if prey are unable to match predator consumption rate, with, for example, reproductive output (Twardochleb et al. 2012; MacNeil et al. 2013).

Although Type II responses were observed in each habitat, there were differences recorded in model parameters. Attack rates were greatest in the most complex habitat treatment and lowest when no habitat was present. As the scaling parameter of the curve, the attack rate describes the slope of the line at the lowest prey densities and therefore provides an indication of predator efficiency at these densities (Hassell and May 1973; Jeschke et al. 2002). The observed attack rates thus reflect the behaviour of a species that is predominantly an ambush predator that seeks out structure (Savino and

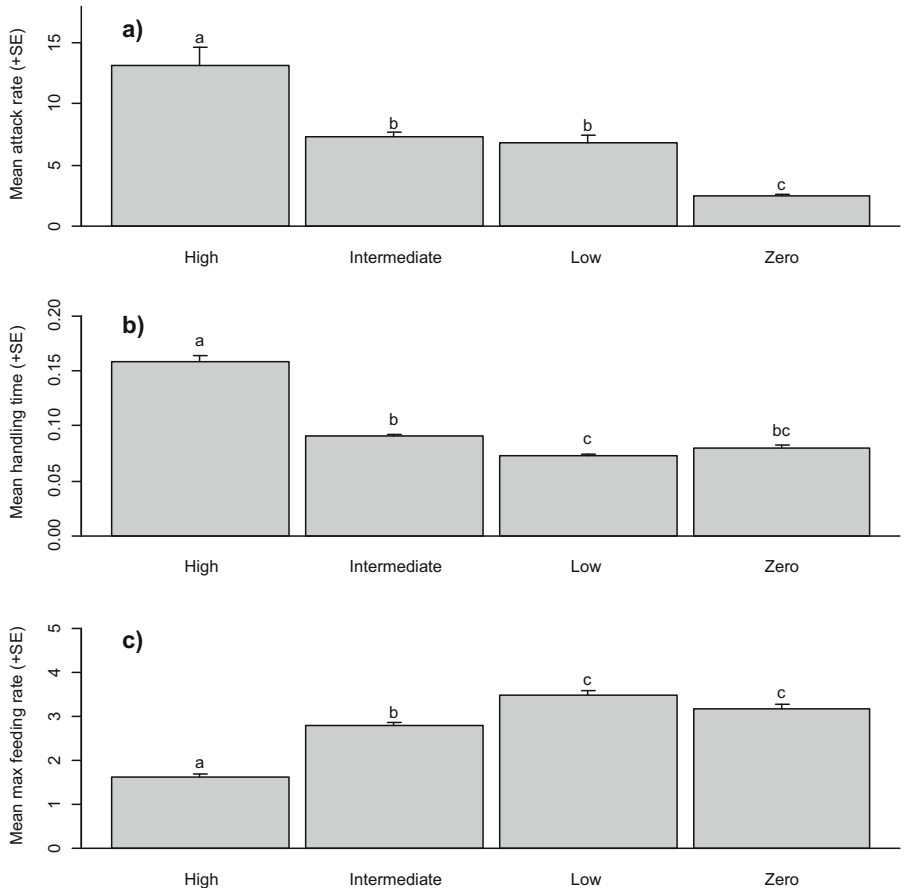

Fig. 3 Mean (+SE) **a** attack rate *a*, **b** handling time *h* and **c** maximum feeding rate $1/hT$ derived from bootstrapping (n=30 each) of juvenile largemouth bass consuming prey in high, intermediate, low and zero complexity simulated habitats. Different letters indicated significant differences (Tukey's contrasts, $p<0.01$)

Stein 1982, 1989b). Juvenile bass in particular may be efficient predators in dense vegetation, with smaller body size permitting comparably easier access to prey than older, larger individuals (Almany 2004b). Thus, the reduction in attack parameter in less complex habitats in comparison to the denser structure in the present study suggests that at low densities, degradation of habitat may in fact provide prey with a reduced mortality risk in comparison to more complex habitats.

As a further reflection of the greater predatory efficiency of juvenile bass at higher prey densities, differences in mean handling times, and thus maximum feeding rates, indicated greater predation at higher prey densities when habitat complexity was reduced. In comparison, high complexity structure reduced maximum feeding rates, suggesting that, although efficient predators at lower densities in these habitats, juvenile bass are impeded overall by such structure. At zero and low habitat complexities, bass were comparably more efficient as indicated by significantly greater feeding rates, therefore with reductions in habitat cover, certain densities of prey are more vulnerable to predation by this species. This may result from the reduction in the physical barrier the habitat complexity provides with simplification in structure (Warfe and Barmuta 2004), or indeed be a consequence of reduced refuge space for prey whereby safe areas become saturated and prey are pushed out into the open where they are more vulnerable to predation (Forrester and Steele 2004).

Type II functional responses can, under certain conditions, be de-stabilising to prey populations and reduce their viability, and indeed at low prey densities in high habitat complexity areas prey populations may be driven to local extinction by juvenile bass as suggested by

the elevated attack rates. Prey populations under such circumstances may, however, be stabilised with the presence of alternative prey whereby as one species becomes rare, the predator switches to feed on another, resulting in a Type III functional response (Akre and Johnson 1979; Elliott 2004). However, field studies consistently suggest that prey populations are heavily impacted by largemouth bass (Godinho and Ferreira 2000; Almeida et al. 2012; Weyl et al. 2013), and we therefore assume that the strength of the Type II responses observed here drives lack of coexistence between bass and native prey as is congruent with other functional response studies that link experimental findings with observed field patterns (Bollache et al. 2008; Dick et al. 2013; MacNeil et al. 2013).

The use of functional responses in a predictive capacity, as applied here, to investigate what may be expected with changes to the environment when important drivers of global change interact, is a further demonstration of the utilisation of this methodology (see Dick et al. 2013, 2014). In this study, the combination of habitat degradation, as simulated with reductions in the density of a plant mimic, and the *per capita* impact of predation by invasive largemouth bass as determined by functional responses, indicates that impacts of the invasive species may potentially be greater with reductions in habitat. Largemouth bass, however, are well established in a number of systems worldwide (Welcomme 1992), and where their removal is not possible, a potential mitigation measure is therefore to focus efforts on the protection of natural vegetation and riparian zones. For further investigation it is suggested that other determinants of invader ecological impacts, such as the numerical response to examine the reproductive and/or aggregative response to prey, are quantified; however, the use of functional responses continues to be a rapid, reliable and in particular predictive assessment of the potential ecological impacts of invasive species in a changing world.

Acknowledgements We thank K. van der Walt, N. Songongo, G. Taylor, A. Luger, B. Ellender, D. Howell, C. Hoek, Y. Omardien, M. Pegg, B. Dredge, L. Mofu, P. Weyl and O. Weyl for technical and logistical support, including field collections. This research was funded by the DST-NRF Centre of Excellence for Invasion Biology. DMR received support from the National Research Foundation (grant 85,417). The Department of Economic Development, Environmental Affairs and Tourism (Cacadu Region) is thanked for issuing research permits (4/13CR & 5/13CR). JD acknowledges support from NERC and the Leverhulme Trust.

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